Electrofishing Catchability of Walleyes, Largemouth Bass, Smallmouth Bass, Northern Pike, and Muskellunge in Wisconsin Lakes

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Abstract.—We sought to determine whether electrofishing catchability was density dependent and varied with physical and biological factors for walleyes Sander vitreus, largemouth bass Micropterus salmoides, smallmouth bass M. dolomieu, northern pike Esox lucius, and muskellunge E. masquinongy in Wisconsin lakes. Electrofishing catch rate (number of fish caught per shoreline mile) was linearly related to population density (number of fish per acre) in spring for largemouth bass, northern pike, and muskellunge and in fall for walleyes, largemouth bass, and smallmouth bass. In contrast, gear saturation caused the electrofishing catch rate to be nonlinearly related (hyperstable) to population density for walleyes and smallmouth bass during spring. Catchability was higher during spring than fall for walleyes, largemouth bass, and smallmouth bass. Catchability of walleyes during fall was positively related to the percentage of littoral zone, whereas catchability of largemouth bass, smallmouth bass, and muskellunge was negatively related to the shoreline development index. Other physical and chemical variables failed to describe significant residual variation in catchability of any other species in any other season. We conclude that population density cannot be accurately estimated from the electrofishing catch rates of walleyes and smallmouth bass during spring. Therefore, mark-recapture methods must still be used to estimate population density if managers choose to sample those species during spring in Wisconsin lakes.

Fisheries surveys often rely on the assumption that the catch rate is linearly related to population density and can therefore be used to index population density via the equation

$$\frac{C}{f} = q \times \frac{N}{A},$$

where C = catch, f = fishing effort, q = catchability, N = fish abundance, and $A = \text{the area occupied by the fish stock when catchability is constant (Ricker 1975; Richards and Schnute 1986; Newby et al. 2000; Hansen et al. 2004). However, gear saturation and nonrandom searching effort may cause catchability to vary with population density (Peterman and Steer 1981; Hansen et al. 2004). Furthermore, tests of nonlinearity between catch rate (<math>C/f$) and population density (N/A) are problematic because density is measured with error, thereby producing biased estimates of catchability when ordinary least-squares (OLS) regression is used (Ricker 1975; Hansen et al. 2004).

Received July 24, 2004; accepted May 10, 2005 Published online October 20, 2005 Finally, precision in estimating catchability varies with environmental and behavioral (seasonal) factors (Hilborn and Walters 1992; Rogers et al. 2003).

The relationship between catch rate and population density can assume three forms: proportionality, hyperstability, and hyperdepletion (Hilborn and Walters 1992). Proportionality occurs when the catch rate increases linearly with population density (q does not change with N/A) because search is random or gear saturation is minimal (Hilborn and Walters 1992). Hyperstability occurs when the catch rate remains high as population density decreases (q is inversely related to N/A) because of nonrandom searching effort or gear saturation (Peterman and Steer 1981; Hilborn and Walters 1992; Hansen et al. 2000). Hyperdepletion occurs when the catch rate decreases at a faster rate than population density (q is directly related to N/A) because the fish respond to the gear, such that highly vulnerable fish within a population are removed more quickly than lessvulnerable fish (Hilborn and Walters 1992).

Population density is measured with error, so the shape of the relationship between catch rate and density is difficult to estimate without bias (Rogers et al. 2003; Hansen et al. 2004). Estimates derived from OLS linear regression are biased be-

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cause OLS regression assumes that the independent X variable (N/A) is measured without error or with much less error than the dependent Y variable (C/f; Ricker 1973; Peterman and Steer 1981; Sokal and Rohlf 1981; Shardlow et al. 1985; Hilborn and Walters 1992). To correctly estimate the shape of the relationship between catch rate and population density, measurement errors in both C/f and N/A must be accounted for when estimating parameters. Geometric-mean functional regression is appropriate if measurement error is similar in the X and Y variables (Ricker 1973, 1975; Sokal and Rohlf 1981). However, if measurement errors differ between the dependent and independent variables, measurement error models and Monte Carlo simulations must be used to account for X-variable measurement errors that are large but not the same as the Y-variable measurement errors (Fuller 1987; Hilborn and Walters 1992; Quinn and Deriso 1999).

Environmental factors affect electrofishing catchability regardless of the form of the relationship between catch rate and population density (Reynolds 1996). Variable water conductivity affects catchability, especially when voltages and amperages are set at standardized levels (Reynolds 1996; Hansen et al. 2004). Water temperature both directly and indirectly affects electrofishing catchability (McInerny and Cross 2000; Hansen et al. 2004) because water conductivity and fish avoidance increase with ambient water temperature (Reynolds 1996). Water temperature can also affect fish location by forcing fish into deeper water when temperatures become stressful and into littoral habitat during diel feeding and spring spawning periods (Bettross and Willis 1988; Reynolds 1996). Lake features such as percent littoral zone and shoreline development index (SDI) also affect electrofishing catchability, because such characteristics describe the amount of shallow-water habitat that can be effectively sampled by electrofishing (Reynolds 1996).

Electrofishing catchability has been evaluated for largemouth bass *Micropterus salmoides* and walleye *Sander vitreus* but has not been previously evaluated for smallmouth bass *M. dolomieu*, northern pike *Esox lucius*, or muskellunge *E. masquinongy*. Density-dependent electrofishing catchability has been found for largemouth bass larger than 200 mm in Minnesota lakes (McInerny and Cross 2000), walleyes in northern Wisconsin lakes during spring (Rogers et al. 2003), and age-0 walleyes in northern Wisconsin lakes during fall (Hansen et al. 2004). The assumed linear form of the

relationship between electrofishing catch rate and density for other fishes (e.g., smallmouth bass, northern pike, and muskellunge) may also be nonlinear but has not been previously evaluated. In addition, the catchability of adult walleyes (Rogers et al. 2003) has only been evaluated in northern Wisconsin and has not been previously evaluated throughout the state.

Potential seasonal differences in catchability have not been examined before. Large handling times (gear saturation) are caused by high catch rates and can lead to density-dependent catchability in assessment fisheries. However, catch rates, and therefore catchability, vary by season (Guy and Willis 1991; Mero and Willis 1992; Pope and Willis 1996; McInerny and Cross 2000). Seasons exhibiting lower catch rates may yield more accurate estimates of population abundance because handling times are generally low, whereas seasons exhibiting high catch rates may yield population abundance estimates that are inaccurate because of large handling times. Evaluations of species-specific seasonal catchability may indicate the season or seasons when electrofishing catch rates can be used to accurately index population abundance.

Our objective was to determine whether electrofishing catchability was density dependent for walleyes, largemouth bass, smallmouth bass, northern pike, and muskellunge in Wisconsin lakes. To evaluate density dependence of electrofishing catchability, we determined whether the electrofishing catch rate was linearly related to population density for each species. First, we used Monte Carlo simulations to account for measurement errors and estimated a bias-corrected slope between electrofishing catch rate and population density. Next, we used analysis of covariance (AN-COVA) to determine whether electrofishing catchability differed between spring and fall seasons. Last, we used multiple regression analysis to determine whether electrofishing catchability varied with physical and biological variables in Wisconsin lakes.

Methods

Walleyes, northern pike (≥14 in), and muskellunge (≥30 in) captured in fyke nets shortly after ice-out were used for marking (fin clips) (Hansen et al. 1991, 2000; Beard et al. 1997; Rogers et al. 2003). The entire lake shoreline was night-electrofished (230-V AC output) 1–2 d after fykenetting to estimate the density of sexually mature walleyes and to mark largemouth bass and small-

TABLE 1.—Species, season, number of Wisconsin lakes sampled (N), and the years for which electrofishing catch rates and population density estimates were used to evaluate catchability models.

Species	Season	N	Years
Walleye	Spring	74	2000-2003
•	Fall	68	2000-2003
Largemouth bass	Spring	28	1999-2003
_	Fall	15	2000-2003
Smallmouth bass	Spring	25	1999-2003
	Fall	11	2000-2003
Northern pike	Spring	18	1985-2000
Muskellunge	Spring	11	1990-1999

mouth bass that were susceptible to electrofishing gear (Hansen et al. 2000; Rogers et al. 2003). Boats were of standard design with two booms, and personnel consisted of two dipnetters and one operator. Mature walleyes were defined as all fish for which sex could be determined and all fish longer than 15 in (Beard et al. 1997; Hansen et al. 2000). Unmarked fish captured during the first electrofishing run were marked by partial removal of one or more fins (Hansen et al. 2000). A second electrofishing survey 2-3 weeks after the first electrofishing sample was used to estimate mature and immature walleye population density and to continue mark-recapture sampling for largemouth bass, smallmouth bass, and northern pike (Hansen et al. 2000). A third (and usually a fourth) electrofishing mark and recapture run during spring was used to complete mark-recapture sampling for largemouth bass, smallmouth bass, and northern pike. Adult muskellunge (≥30 in) were captured in two consecutive years by use of the methods described by Margenau and AveLallemant (2000; Table 1).

An electrofishing run during fall targeted age-0 walleyes, but since 2000 fall electrofishing has also targeted age-1 and older walleyes and other species including largemouth bass, smallmouth bass, northern pike, and muskellunge (Hansen et al. 2004). Fall electrofishing data were used only when comments on the data sheet indicated that all species were collected during sampling. Northern pike and muskellunge fall electrofishing data and corresponding population estimates were available for less than 10 lakes and thus were not evaluated in this study. Furthermore, age-0 walleyes were removed from fall catch rates to eliminate recruitment between spring and fall sampling periods. The number of fish caught on the last recapture run was used to estimate catch rate. The second electrofishing recapture run (which targeted total walleye density) was used to estimate walleye catch rate. The third and usually the fourth electrofishing recapture runs were used to estimate largemouth bass and smallmouth bass catch rates. For example, if four recapture runs were completed, the number of fish captured on the fourth run was used to estimate the catch rate.

Density was estimated by use of Chapman's modification of the Peterson estimator for single recapture runs, and the modified Schnabel estimator was used for multiple recapture runs (Ricker 1975). The population densities of walleyes during spring and fall, largemouth bass during fall, smallmouth bass during fall, and muskellunge (≥30 in) during spring were estimated by use of Chapman's modification of the Peterson estimator (Ricker 1975; Hansen et al. 2000). The spring population densities of largemouth bass, smallmouth bass, and northern pike (≥14 in) were estimated with the modified Schnabel estimator (Ricker 1975).

Spring and fall electrofishing catch rates (fish/mi of shoreline) of walleyes, largemouth bass, smallmouth bass, northern pike, and muskellunge were modeled as nonlinear functions of their respective population densities (fish/acre) based on the following model:

$$\frac{C}{f} = \alpha \times \left(\frac{N}{A}\right)^{\beta+1} e^{\varepsilon},$$

where α is an estimate of catchability at low population density, β is the degree of curvature between C/f and N/A, and ε is the error (Peterman and Steer 1981). When β is equal to 0, the relationship between catch rate and density is linear (proportional). When β is less than 0, density increases at a faster rate than catch rate (hyperstability). When β is greater than 0, catch rate increases at a faster rate than density (hyperdepletion). Parameters were estimated from the \log_{ε} transformed model

$$\log_e\left(\frac{C}{f}\right) = b_0 + b_1 \log_e\left(\frac{N}{A}\right) + \varepsilon,$$

where the intercept $b_0 = \log_e \alpha$ and the slope $b_1 = \beta + 1$. When $b_1 = 1$, catch rate is linearly related to density (proportional); when b_1 is less than 1, density increases faster than catch rate (hyperstability); and when b_1 is greater than 1, catch rate increases faster than density (hyperdepletion).

Estimates of catch rate and population density were both measured with error, so Monte Carlo simulations were used to estimate the biascorrected slopes and intercepts of the relationships between catch rate and population density for each of the eight models tested (Table 1; Rogers et al. 2003; Hansen et al. 2004). First, linear regression was used to estimate the slope (b_{ols}) of the relationship between catch rate and density for each model. Second, 1,000 random values of the total number of recaptured fish ($\lambda = \Sigma R$) were generated from a Poisson distribution by use of the random number generation function in the data analysis tool pack of Microsoft Excel (Microsoft Corp. 2004). The use of a Poisson distribution was warranted in this study because the total number of recaptures (ΣR) was small (Ricker 1975). This produced 1,000 random values of the total number of recaptured fish for every lake used in each model. Third, the randomly generated recapture values were used to calculate 1,000 estimates of abundance (N) by use of Chapman's modification of the Peterson estimator (single recapture run estimates) or the modified Schnabel estimator (multiple recapture run estimates). Fourth, each estimate of N (1,000 per lake) was converted to density (N/A) by dividing by lake surface area (acres). Fifth, each of the 1,000 random density values was regressed against the appropriate electrofishing catch rate for that particular model by use of OLS regression to estimate 1,000 biased slopes and intercepts for each model (b_{mc}). Last, the bias-corrected slope and intercept (b_{bc}) were estimated for each of the eight models tested by means of the equation

$$b_{\rm bc} = b_{\rm ols} + (b_{\rm ols} - b_{\rm mc}),$$

where $b_{\rm ols}$ is the OLS regression slope or intercept estimate and $b_{\rm mc}$ is the estimated slope or intercept from the 1,000 linear regressions that used simulated values of population density.

To evaluate the linearity of the relationship between electrofishing catch rate (y-axis) and population density (x-axis), we used the distribution of the bias-corrected estimates to empirically determine the median and 95% confidence interval for the slope and intercept. Bias-corrected slope estimates were tested for significant differences from 1 (i.e., to indicate density-dependent catchability) by use of the upper and lower 0.025th percentiles of the distribution of bias-corrected slopes (i.e., 95% confidence intervals). The linearity of the relationship between catch rate and population density estimates was tested for walleyes, largemouth bass, and smallmouth bass during spring and fall and for northern pike and muskellunge during spring.

The measurement error ratio between electro-

fishing catch rate and population density was estimated for walleyes, largemouth bass, and small-mouth bass during spring and fall and for northern pike and muskellunge during spring with an errors-in-variables model of the form

$$\hat{\beta}_1 m_{xy} - \hat{\beta}_1 (m_{yy} - \delta m_{xx}) - \delta m_{xy} = 0,$$

where $\hat{\beta}_1$ is the bias-corrected slope, m_{YY} is the estimated variance in Y, m_{XX} is the estimated variance in X, m_{XY} is the estimated covariance between X and Y, and Y is the Y/X measurement error ratio, which is estimated iteratively (Fuller 1987; Quinn and Deriso 1999).

We modeled factors that may have affected electrofishing catchability by incorporating environmental factors into the equation that describes the relationship between electrofishing catch rate and population density, that is,

$$\frac{C}{f} = \alpha \left(\frac{N}{A}\right)^{\beta+1} X_1^{b_2} \cdots X_n^{b_n} e^{\varepsilon},$$

where the X variables were SDI (shoreline length in miles/ $\{2 \times [\pi \times A \text{ in square miles}]^{0.5}\}$), specific conductance (μ S/cm, measured at 77°F), percent littoral zone (percentage of lake surface area ≤ 20 ft deep), water temperature (°F; fall walleyes only), and Secchi depth (ft; spring muskellunge only; Table 2). Lake data were obtained from the Wisconsin Surface Water Inventory database and Surface Water Resource publications, except for water temperature, which was measured during sampling (Wisconsin Conservation Department 1961–1966; Wisconsin Department of Natural Resources 1967–1983; Nate et al. 2003). Parameters were estimated from the \log_e transformed equation

$$\log_e\left(\frac{C}{f}\right) = b_0 + b_1 \log_e\left(\frac{N}{A}\right) + b_2 \log_e X_1 + \cdots + b_n \log_e X_n + \varepsilon,$$

where $b_0 = \log_e \alpha$, the slope $b_1 = \beta + 1$, and slopes b_2 to b_n are coefficients that describe how each X variable affected catchability (Hansen et al. 2000). Models were fitted by use of backward stepwise linear regression, where explanatory variables were rejected if P > 0.05, were added if $P \le 0.05$, and were retained in the final model if $P \le 0.05$.

Behavioral factors that may have caused catchability to differ between seasons were modeled by use of ANCOVA. Both the catch rate and population density were \log_e transformed to meet the assumption of normality, and season (spring or

TABLE 2.—Sample size (N) and minimum, maximum, and mean values of physical characteristics used for each species and season model to predict electrofishing catchability in Wisconsin lakes. Variables are shoreline development index (SDI; shoreline length in miles/ $\{2 \times [\pi \times \text{area in square miles}]^{0.5}\}$); specific conductance (SC; μ S/cm, measured at 77°F); percent littoral zone (percentage of lake surface area \leq 20 ft deep); water temperature (°F); and Secchi depth (ft).

Species	Season	Variable	N	Minimum	Maximum	Mean
Walleye	Spring	% Littoral	62	10.0	100.0	71.32
		SDI	73	1.1	5.5	2.40
		SC	72	16.0	270.0	88.91
	Fall	% Littoral	57	15.0	100.0	73.19
		SDI	67	1.1	5.5	2.45
		SC	67	16.0	270.0	87.88
		Water temperature	66	46.0	69.0	58.96
Largemouth bass	Spring	% Littoral	25	15.0	100.0	65.12
		SDI	26	1.1	4.1	1.96
		SC	25	16.0	250.0	99.92
	Fall	% Littoral	13	15.0	100.0	68.08
		SDI	14	1.1	3.1	1.88
		SC	14	27.0	250.0	95.43
Smallmouth bass	Spring	% Littoral	21	10.0	100.0	58.14
		SDI	24	1.1	4.1	2.06
		SC	24	16.0	192.0	87.08
	Fall	% Littoral	8	15.0	100.0	69.00
		SDI	10	1.3	3.1	2.10
		SC	10	25.0	110.0	70.40
Northern pike	Spring	% Littoral	15	35.0	100.0	72.93
		SDI	18	1.2	3.0	1.75
		SC	18	30.0	401.0	155.94
Muskellunge	Spring	SDI	11	1.0	3.0	2.02
		SC	11	63.0	127.0	91.64
		Secchi depth	11	2.0	25.0	11.64

fall) was treated as the covariate, giving the following equation:

$$\begin{split} \log_e\!\left(\!\frac{C}{f}\!\right) &= b_0 \,+\, b_1 \!\log_e\!\left(\!\frac{N}{A}\!\right) + \, b_2 \text{Season} \\ &+\, b_3 \!\log_e\!\left(\!\frac{N}{A}\!\right) \times \, \text{Season} \,+\, \epsilon. \end{split}$$

Spring and fall were considered to be different if slopes differed significantly (P < 0.05) between seasons ($b_3 \neq 0$; $\beta_S \neq \beta_F$) or if the slopes were homogeneous but the intercepts differed significantly between seasons ($b_2 \neq 0$; $\alpha_S \neq \alpha_F$). Catch-

ability was considered to be similar between spring and fall if the slopes $(b_3 = 0)$ and intercepts $(b_2 = 0)$ did not differ significantly between seasons.

Results

Population density and electrofishing catch rate varied among species and between seasons in Wisconsin lakes (Table 3). Mean population density was highest for walleyes during fall and lowest for muskellunge during spring (Table 3). In contrast, the mean electrofishing catch rate was highest for northern pike during spring and lowest for muskellunge during spring (Table 3). Population denseting the spring of the season of the season

TABLE 3.—Mean, minimum, and maximum electrofishing catch rates and population densities for walleyes, largemouth bass, smallmouth bass, northern pike, and muskellunge in Wisconsin lakes.

			Catch rate (fish/mile)			Density (fish/acre)			
Species	Season	N	Mean	Minimum	Maximum	Mean	Minimum	Maximum	
Walleye	Spring	74	18.81	0.28	78.16	10.67	0.01	60.48	
	Fall	68	10.68	0.12	119.01	11.20	0.01	60.48	
Largemouth bass	Spring	28	15.11	0.08	91.53	6.95	0.04	50.99	
	Fall	15	6.74	0.28	26.21	7.13	0.04	50.99	
Smallmouth bass	Spring	25	8.50	1.11	36.07	1.98	0.24	11.61	
	Fall	11	3.44	0.22	16.57	1.51	0.26	5.61	
Northern pike	Spring	18	21.28	2.74	51.11	5.85	1.14	11.77	
Muskellunge	Spring	11	1.99	0.18	7.06	0.35	0.12	0.55	

TABLE 4.—Measurement error ratio (Y/X), bias-corrected slope ($\beta + 1$), and catchability coefficient (α) estimated from the catchability equation among species and between seasons in Wisconsin lakes (95% CI = 95% confidence interval).

				$\beta + 1$	α		
Species	Season	Y/X	Estimate	95% CI	Estimate	95% CI	
Walleye	Spring	3.38	0.75	0.61-0.88	2.89	2.26-3.68	
	Fall	6.94	0.83	0.62 - 1.04	0.93	0.63 - 1.37	
Largemouth bass	Spring	0.79	0.88	0.69 - 1.06	3.04	2.52 - 3.67	
	Fall	1.79	0.62	0.16 - 1.08	1.41	0.90 - 2.21	
Smallmouth bass	Spring	1.96	0.57	0.23-0.90	5.40	5.22-5.61	
	Fall	10.68	0.45	-0.48 - 1.37	1.72	1.81 - 1.64	
Northern pike	Spring	8.44	0.77	0.22 - 1.33	4.87	2.00-11.86	
Muskellunge	Spring	8.98	1.60	0.78 - 2.40	8.54	3.34-21.86	

sities were similar during spring and fall for walleyes, largemouth bass, and smallmouth bass, whereas catch rates were greater during spring than fall for these same species (Table 3).

Electrofishing catch rate was linearly related to population density during spring for three of the five species examined and during fall for the three species examined (Table 4). The electrofishing catch rate was linearly related to population density (proportional) of walleyes during fall (Figure 1), largemouth bass during spring and fall (Figure 2), smallmouth bass during fall (Figure 3), and northern pike and muskellunge during spring (Figure 4). In contrast, the electrofishing catch rate was nonlinearly related to the spring population density (hyperstable) of walleyes (Figure 1) and smallmouth bass (Figure 3).

Catchability varied among species and between seasons in Wisconsin lakes (Table 4). Catchability was highest for muskellunge during spring and lowest for walleyes during fall, which explains why catch rate patterns did not parallel population density patterns (Table 4). Catchability was greater during spring than fall for walleyes, largemouth bass, and smallmouth bass, which explains why catch rates were greater during spring than fall for these species.

Measurement error ratios between electrofishing catch rate and population density varied among species and between seasons in Wisconsin lakes (Table 4). Measurement error ratios between electrofishing catch rate and population density were highest for smallmouth bass during fall and lowest for largemouth bass during spring. Seven of eight measurement error ratios were greater than 1.0, indicating that catch rates were measured with more error than population density was. Furthermore, measurement error ratios were greater during fall than spring for walleyes, largemouth bass, and smallmouth bass; this suggests that catch rates

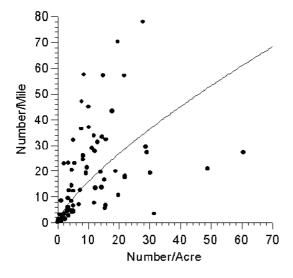
were measured with greater error during fall than spring (Table 4). Measurement error ratios were two times greater during fall than spring for walleyes and largemouth bass and were five times greater during fall than spring for smallmouth bass (Table 4).

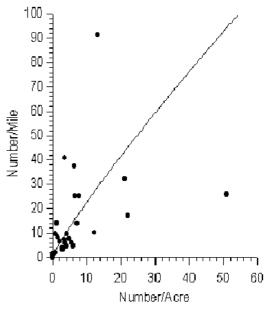
Catchability was significantly greater during spring than fall for walleyes, largemouth bass, and smallmouth bass (Tables 4, 5). The curvature (slope) of the relationship between $\log_e(C/f)$ and $\log_e(N/A)$ did not differ significantly between spring and fall for walleyes, largemouth bass, or smallmouth bass (Table 5). In contrast, electrofishing catchability (intercept of the relationship between $\log_e[C/f]$ and $\log_e[N/A]$) was significantly greater during spring than fall for walleyes, largemouth bass, and smallmouth bass (Table 5). Catchability was three times greater during spring than fall for walleyes and smallmouth bass and two times greater during spring than fall for largemouth bass (Table 4).

Electrofishing catchability was significantly affected by percent littoral zone, specific conductance, and SDI in Wisconsin lakes (Table 6). During fall, the catchability of walleyes was positively related to percent littoral zone. During spring, catchability was negatively related to SDI for largemouth bass, smallmouth bass, and muskellunge (Table 6). The catchability of northern pike in spring was negatively related to percent littoral zone and specific conductance (Table 6). Other physical and chemical variables failed to account for significant variation in catchability of any other species in any other season (Table 6).

Discussion

We found that catch rates and catchability were higher during spring than fall for walleyes, largemouth bass, and smallmouth bass; these findings were probably due to spawning behavior. Electro-





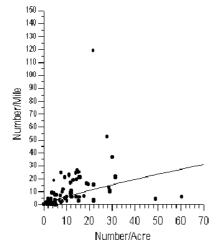


FIGURE 1.—Electrofishing catch per shoreline mile as a function of population density for walleyes in Wisconsin lakes during spring (upper panel) and fall (lower panel) of 2000–2003. The solid line represents the biascorrected line.

fishing catch rates were greater during spring than fall for 8-in or longer largemouth bass in 12 Minnesota lakes (McInerny and Cross 2000) and walleyes and saugeyes (walleye × sauger *S. canadensis*) in an Ohio reservoir (Johnson et al. 1988) because fish were concentrated in the littoral zone during spring to spawn. We also found that electrofishing catch rates and catchability in Wisconsin lakes were greater during spring than fall because

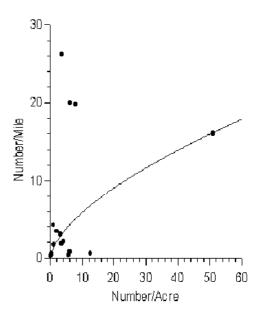
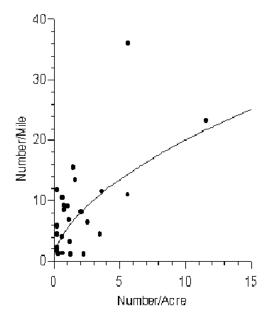


FIGURE 2.—Electrofishing catch per shoreline mile as a function of population density for largemouth bass in Wisconsin lakes during the spring of 1999–2003 (upper panel) and the fall of 2000–2003 (lower panel). The solid line represents the bias-corrected line.



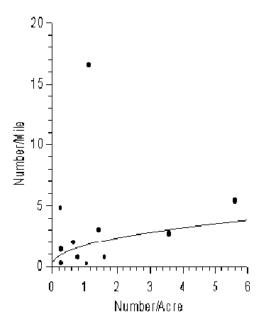
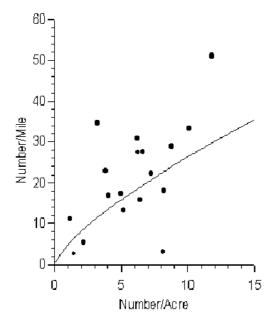


FIGURE 3.—Electrofishing catch per shoreline mile as a function of population density for smallmouth bass in Wisconsin lakes during the spring of 1999–2003 (upper panel) and the fall of 2000–2003 (lower panel). The solid line represents the bias-corrected line.

fish were concentrated in the littoral zone to spawn and were more susceptible to electrofishing capture (Hall 1986; Pope and Willis 1996). In contrast, electrofishing catch rates were similar between spring and fall for largemouth bass in a South Dakota impoundment because quality-length bass (≥12 in) moved into the littoral zone during fall to find optimal temperatures and/or prey (Bettross and Willis 1988).

We found evidence of both density-independent and density-dependent catchability between electrofishing catch rate and population density, as in other studies and with different capture methods (Peterman and Steer 1981; Hall 1986; Hill and Willis 1994; McInerny and Cross 2000). Electrofishing catch rates were linearly related to population density of largemouth bass in a Wisconsin lake (Coble 1992), 12 Ohio impoundments (Hall 1986), and 12 South Dakota impoundments (Hill and Willis 1994). In our study, search effort was probably random and gear saturation was probably minimal for walleyes during fall, largemouth bass during spring, largemouth bass during fall, smallmouth bass during fall, northern pike during spring, and muskellunge during spring because catchability was density independent (Hilborn and Walters 1992). Searching effort was random and gear saturation was minimal because the entire lake shoreline was sampled and dipnetting efficiency did not decrease with increasing population density. In comparison, electrofishing dipnetting efficiency decreased as density increased for largemouth bass during spring in 12 Minnesota lakes (McInerny and Cross 2000), for walleyes during spring in Wisconsin lakes (Rogers et al. 2003), and for age-0 walleyes during fall in Wisconsin lakes (Hansen et al. 2004). In our study, gear saturation or nonrandom searching could have occurred for walleyes and smallmouth bass during spring because dipnetting efficiency decreased through gear saturation as population density increased (Peterman et al. 1985; McInerny and Cross 2000; Rogers et al. 2003). Nonrandom searching cannot explain density-dependent electrofishing catchability in Wisconsin lakes, as crews sampled entire lake shorelines.

Electrofishing catchability of walleyes during spring ($\alpha = 2.9$) in lakes located throughout Wisconsin in our study was lower than previously found for walleyes during spring (6.0) in northern Wisconsin lakes (Rogers et al. 2003). The electrofishing catchability of other species in spring and fall in lakes throughout Wisconsin (0.1–8.5) was generally lower than that of age-0 walleyes (8.6)



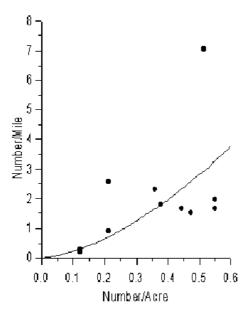


FIGURE 4.—Electrofishing catch per shoreline mile as a function of fish population density in Wisconsin lakes for northern pike during the spring of 1985–2000 (upper panel) and for muskellunge during the spring of 1990–1999 (lower panel). The solid line represents the biascorrected line.

in northern Wisconsin lakes (Hansen et al. 2004). Surprisingly, we found that electrofishing catchability of walleyes during spring in lakes located throughout Wisconsin was lower than that found in northern Wisconsin lakes (Rogers et al. 2003), perhaps because environmental and behavioral factors differed between years (our study: 2000–2003; Rogers et al. 2003: 1990–2000) and locations.

Measurement error ratios (Y/X) between electrofishing catch rate and population density were greater than 1.0 for seven of the eight species × season combinations evaluated, as was found in similar studies of electrofishing catchability (Rogers et al. 2003; Hansen et al. 2004). Measurement error ratios were also greater than 1.0 for walleye electrofishing catch rate versus population density during spring in northern Wisconsin lakes (measurement error ratios = 3.46-28.51; Rogers et al. 2003) and for age-0 walleyes during fall in northern Wisconsin lakes (measurement error ratio = 9.032; Hansen et al. 2004) because the electrofishing catch rate was measured with greater error than density. We also found that the measurement errors of electrofishing catch rate were greater than those of population density estimated by markrecapture methods (measurement error ratios = 1.786–10.676). Therefore, OLS regression may provide nearly unbiased estimates of intercepts and slopes when measurement errors are greater for estimates of electrofishing catch rate (y-axis) than for estimates of population density (x-axis; Hansen et al. 2005).

Electrofishing catchability in Wisconsin lakes was significantly affected by percent littoral zone, specific conductance, and SDI, as was similarly reported by Rogers et al. (2003). For example, electrofishing catchability was positively related to percent littoral zone and adult walleye (>15 in) population density in northern Wisconsin lakes because walleyes were more susceptible to capture by littoral sampling methods (e.g., fyke nets) in lakes with shallow slopes (Rogers et al. 2003). Similarly, we found that fall electrofishing catchability of walleyes in Wisconsin lakes was positively related to percent littoral zone, probably because electrofishing efficiency is related to the amount of littoral habitat in which electrofishing is effective (Reynolds 1996). In contrast, we found that electrofishing catchability was negatively related to SDI for largemouth bass, smallmouth bass, and muskellunge during spring. The increase in catchability as SDI decreased can be explained by the fact that lakes with lower SDI have steep, slop-

TABLE 5.—Test statistics from analysis of covariance comparing electrofishing catchability of walleyes, largemouth bass, and smallmouth bass between spring and fall seasons in Wisconsin lakes.

		Slope			Intercept				
Species	F	df	P	F	df	Р			
Walleye Largemouth bass Smallmouth bass	0.55 0.715 0.19	1, 132 1, 26 1, 18	0.458 0.405 0.666	36.8 6.137 18.19	1, 133 1, 27 1, 19	<0.0001 0.019 <0.0004			

TABLE 6.—Sample size (N; number of lakes), coefficient of determination (r^2), coefficient estimates, and test statistics from backward stepwise regression models that examined the effects of physical and chemical variables on electrofishing catchability of walleyes, largemouth bass, and smallmouth bass during spring and fall and the catchability of northern pike and muskellunge during spring in Wisconsin lakes. The N and r^2 values are relevant to significant-variable models only. Coefficients are defined as follows: α , catchability; $\beta + 1$, bias-corrected slope; shoreline development index (SDI; shoreline length in miles/ $\{2 \times [\pi \times \text{area in square miles}]^{0.5}\}$); specific conductance (SC; μ S/cm, measured at 77°F); percent littoral zone (percentage of lake surface area \leq 20 ft deep); water temperature (°F); and Secchi depth (ft).

Species	Season	N	r^2	Coefficient	Estimate	SE	T	P
Walleye	Spring	74	0.57	α	3.241	0.153	7.669	< 0.0001
				$\beta + 1$	0.68	0.069	9.895	< 0.0001
				% Littoral	0.206	0.175	1.178	0.244
				SDI	-0.097	0.245	-0.398	0.692
				SC	-0.031	0.183	-0.168	0.867
	Fall	57	0.47	α	0.034	1.258	-2.698	0.009
				$\beta + 1$	0.704	0.103	6.847	< 0.0001
				% Littoral	0.82	0.29	2.822	0.006
				SDI	0.135	0.373	0.360	0.720
				SC	-0.257	0.285	-0.901	0.372
				Water temperature	-1.167	1.828	-0.639	0.526
Largemouth bass	Spring	26	0.80	α	11.485	0.349	6.982	< 0.0001
				$\beta + 1$	0.691	0.078	8.854	< 0.0001
				SDI	-1.843	0.481	-3.327	0.0004
				% Littoral	-0.013	0.278	-0.048	0.962
				SC	-0.464	0.240	-1.938	0.066
	Fall	13	0.19	α	1.675	0.407	1.270	0.277
				$\beta + 1$	0.444	0.212	2.092	0.057
				% Littoral	1.144	0.717	1.595	0.142
				SDI	-1.509	1.432	-1.054	0.314
				SC	0.407	0.738	0.551	0.593
Smallmouth bass	Spring	24	0.28	α	12.073	0.446	5.578	< 0.0001
				$\beta + 1$	0.429	0.161	2.664	0.014
				SDI	-1.181	0.606	-1.949	0.064
				% Littoral	0.188	0.252	0.748	0.464
				SC	-0.093	0.264	0.353	0.728
	Fall	11	0.00	α	1.716	0.401	1.348	0.211
				$\beta + 1$	0.386	0.408	0.944	0.370
				% Littoral	-0.406	0.902	-0.449	0.672
				SDI	-0.387	2.054	-0.189	0.856
				SC	-0.108	0.740	-0.146	0.888
Northern pike	Spring	15	0.80	α	188,150	1.447	8.393	< 0.0001
				$\beta + 1$	0.866	0.170	5.094	0.0004
				SC	-1.027	0.153	-6.721	< 0.0001
				% Littoral	-1.383	0.275	-5.038	0.0004
				SDI	0.317	0.332	0.954	0.363
Muskellunge	Spring	11	0.80	α	16.232	0.405	6.877	0.0001
•				$\beta + 1$	1.39	0.248	5.604	0.0005
				SDI	-1.342	0.407	-8.298	0.0108
				SC	0.107	0.767	0.140	0.893
				Secchi depth	0.326	0.204	1.592	0.155

ing banks, thereby concentrating fish in the available littoral habitat during spring spawning, which results in higher spring catchability estimates.

We also found that spring electrofishing catchability of northern pike was significantly related to percent littoral zone and specific conductance, as was shown for other species (Hill and Willis 1994; Rogers et al. 2003; Hansen et al. 2004). Our finding that specific conductance was related to electrofishing catchability for northern pike but not for the other four species may be attributable to the difference in conductivity between northern pike and the other species (Miranda and Dolan 2003). Power (when electrofishing) is most effectively transferred to the fish when the water conductivity and fish conductivity are equal (Kolz and Reynolds 1990; Reynolds 1996; Miranda and Dolan 2003). Among-species difference in fish conductivity and fish size could cause the difference between water conductivity and fish conductivity to vary (Kolz and Reynolds 1990; Reynolds 1996; Miranda and Dolan 2003). This, in turn, would create differences in the effectiveness of electrofishing, and therefore electrofishing catchability, for different species when standardized sampling regimes are used to target multiple species (Miranda and Dolan 2003). For this study, we used the most current specific conductance data available. However, our results could be affected by changes in specific conductance data that were collected in the years prior to the mark-recapture surveys.

Management Implications

Estimation of population density from electrofishing catch rate is less costly and more efficient than mark-recapture methods, so more water bodies can be sampled at a lower cost (Hall 1986; Coble 1992; McInerny and Degan 1993; Hill and Willis 1994). However, electrofishing catch rate should only be used to estimate population density when catchability is density independent and when the effects of confounding environmental variables are known (McInerny and Cross 2000). Population density in Wisconsin lakes can be estimated from catch rate by dividing catch rate by the catchability coefficient for walleyes during fall, largemouth bass during spring and fall, smallmouth bass during fall, northern pike during spring, and muskellunge during spring. We recommend that sampling in Wisconsin lakes should occur during fall for walleyes and smallmouth bass and during spring for largemouth bass, northern pike, and muskellunge because catchability was found to be density independent. However, fishery managers must always be cognizant of the possibility that catchability is density dependent and must therefore evaluate the linearity of relationships between catch rate and population density and quantify the effects of behavioral and environmental factors on catchability before using catch rates to estimate population density (Hansen et al. 2004). Electrofishing catch rate should not be used to estimate population density when catchability is density dependent or when confounding environmental variables are unknown (Hansen et al. 2004). Therefore, mark-recapture methods should still be used in Wisconsin lakes to estimate the population density of walleyes and smallmouth bass if managers choose to sample these species during spring.

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